Feeding and Growth of *Octopus dofleini* (Wülker)

BY

B. HARTWICK, L. TULLOCH [1] AND S. MACDONALD [2]

Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6

(3 Text figures)

INTRODUCTION

Octopus dofleini (Wülker) IS A LARGE OCTOPUS inhabiting coastal waters on the west coast of North America. MOTTET (1975) has reviewed some of the extensive literature on the fisheries biology of this octopus in Japanese waters. Although less is known about its habits on the west coast of North America, the potential of this octopus to support a limited fishery has been recognized (PENNINGTON, 1979; HARTWICK *et al.*, 1978a; R. Clifton, Washington State, personal communication). Field studies of *O. dofleini* on the west coast have included aspects of natural history and behaviour (HARTWICK *et al.*, 1978b, 1978c; KYTE & COURTNEY, 1977; HIGH, 1976a, b; JOHNSON, 1942) but relatively little is known of its feeding ecology and growth. Feeding and growth studies have been carried out for several other species of octopuses (see, for example, NIXON, 1966; VAN HEUKELEM, 1973, 1976; HANLON, 1977; JOLL, 1977; MATHER, 1980). Most of these studies have been restricted to the laboratory and the extent of such laboratory studies of one species, *Octopus vulgaris* Cuvier, is reflected in the recent book by WELLS (1978). Considerably less work has been done on octopuses in their natural environment, although there are exceptions (KAYES, 1974; HOCHBERG & COUCH, 1970; YARNELL, 1969; ALTMAN, 1967; WOODS, 1965). An indirect study of predation by octopuses has been reported (FOTHERINGHAM, 1974) but, in general, detailed information on feeding and growth under natural conditions is lacking.

The present study was initiated to obtain data on the feeding and growth of *Octopus dofleini* in its natural habitat. Aspects of diet and its variation were considered along with predator-size relationships. Short term growth experiments were also carried out and are discussed in relation to similar studies with other species.

---

[1] Vancouver Public Aquarium, P. O. Box 3232, Vancouver, B. C.

[2] Department of Zoology, University of Western Ontario, London, Ontario

MATERIALS AND METHODS

The study was carried out in Barkley and Clayoquot Sounds on the west coast of Vancouver Island, British Columbia. Information was gathered in 3 ways; collections of shells at octopus dens, tagging and recapture of octopuses in the field, and growth studies of captive octopuses.

Shells from octopus dens were collected from January through August, 1977, using SCUBA at 12 different sites within the 2 sounds. A total of 117 different dens was examined. After dens were located they were checked for prey items on a monthly basis from then on. Nine dens were checked at least weekly for more accurate information on feeding rates. Each collection of shells was accompanied by a record of the den site, its depth and date of collection. These factors were used in a multiple regression analysis to determine their relative contribution to the variation in the percentage of particular items in the diet. Significance was determined at the 5% level unless otherwise indicated.

To compare octopus size with prey size, the wet weights were estimated for 50 octopuses. This usually involved taking the octopus to the surface and obtaining a weight with a spring scale. In a few cases where an octopus escaped or remained in the den, its weight was estimated from the appearance of the octopus. This method was fairly accurate, although an error of 5 or even 10 kg might be expected in larger individuals. Prey items found at the dens were taken to the surface and measured with vernier calipers.

Although no quantitative estimates of prey availability were made, the presence and relative abundance of potential prey items were noted.

Information on the growth of octopuses was available through a tag and recapture program initiated in Clayoquot Sound in 1978. Individual octopuses were taken to the surface, weighed, sexed and then tagged with a Petersen disc at the base of one arm. These tags, commonly used on fish, were attached by inserting a pin through the arm. The tagged octopuses were taken back to their dens and released. In all cases tagged individuals moved back into their dens with no apparent effects from the tagging operation.

Additional information on growth and feeding came from experiments with captive octopuses. In July and August, 1977, 2 octopuses weighing 1.1 kg and 18.2 kg were placed in large aquaria (2.6 x 1.3 x 1 m) in running sea water in the Bamfield Marine Station at Bamfield, British Columbia. Observations were made on their feeding response to various freshly collected bivalves.

In October, 1978, 4 wild-caught octopuses were placed in running sea water (temp. 10-13° C) in separate aquaria (96 L tanks) at the marine station while 2 others were placed in a large partitioned box (117 L) with a plexiglass bottom and suspended from floats 1.5 m below the surface in Bamfield Inlet (Barkley Sound). The box had mesh-covered holes for water circulation. Surface temperatures in the inlet varied from 15° C in early October to 7.5 C in December.

The 4 octopuses in the aquaria were fed filleted hake, *Merluccias productus* (Ayres, 1855) and live kelp crabs, *Pugettia producta* Randall, 1839; just over 1% of body weight per day was made available. At times only hake or only crab was made available to see if the feeding rate was altered in comparison with that when both foods were available. Octopuses in the box suspended in the inlet were fed *ad libitum* on both *M. productus* and *P. producta* and also abalone *Haliotis kamtschatkana* Jonas, 1845 and the bivalves *Mya arenaria* Linnaeus, 1758, and *Protothaca staminea* (Conrad, 1837). The responses of the octopuses to these various food items were observed through the plexiglass bottom of the box. All remains were removed daily. All shells, crab exoskeletons and prey were weighed. Wet weights of octopuses were taken with a spring balance every 14 days. No anaesthetic was used during the weighing but the animals were suspended until excess water dripped off and gentle pressure was applied to remove water from the mantle cavity. Although some water undoubtedly remained in the mantle cavity the procedure was consistent with each octopus and was considered as minimum stress. Weighings of octopuses in the laboratory were less frequent than those in the box suspended in the inlet. Calculations of growth and feeding parameters were as follows,

$$\text{Daily growth rate} = \frac{W_2 - W_1}{t\overline{W}} \times 100$$

$$\text{Daily feeding rate} = \frac{I}{t\overline{W}} \times 100$$

$$\text{Food conversion} = \frac{W_2 - W_1}{I} \times 100$$

$$\text{Conversion ratio} = \frac{1}{\text{food conversion}}$$

where W_1 is the initial weight of an octopus, W_2 is the final weight, $\overline{W}$ is the average weight over observation period t, and I is the weight of food eaten. The formulae come from Nixon (1966), Van Heukelem (1973), Joll (1977) and Wells (1978). Food conversion is synonymous with food uptake (Nixon, 1966) and gross growth efficiency (Joll, 1977).

RESULTS

DIET of OCTOPUSES

Based on shell collections from dens in both Barkley and Clayoquot Sound, octopuses fed most frequently on bivalves and crabs. In particular, the cockle *Clinocardium nuttallii* (Conrad, 1837), the littleneck clam *Protothaca staminea* and crabs in the genus *Cancer* occurred frequently in the diet. The rest of the diet consisted of various molluscs and other organisms (Table 1).

The composition of shells at dens varied in both space and time. Regional differences showed up when collections from dens in Barkley Sound were compared with those from Clayoquot Sound. In Barkley Sound, the bivalve *Protothaca staminea* formed the greatest part of the diet (28%, N = 1478) along with crabs, mainly *Cancer productus,* which accounted for 19% of the items at dens. Octopuses in Clayoquot Sound fed mainly on *Clinocardium nuttallii* (41%, N = 1014) along with crabs (Figure 1).

In Clayoquot Sound, feeding on *Clinocardium nuttallii* remained generally high throughout the summer with increasing use of rock crabs, *Cancer productus* as well. The use of *Protothaca staminea* in this area remained relatively low throughout the study period. In Barkley Sound, feeding on the crab *C. productus* increased over the summer along with continuing dependence on *P. staminea.* In contrast to its heavy use in Clayoquot Sound, *C. nuttallii* appeared in only small numbers in dens in Barkley Sound.

There is evidence of individual differences in the feeding habits of octopuses. At times individual octopuses in the

Table 1

The diet of octopuses based on collections of shells at dens. Prey items are expressed as a % of total number (3492) of items found in all dens. Most are molluscs with other phyla indicated by superscript.

Prey item	%
Clinocardium nuttallii (Conrad, 1837)	28.81
Cancer spp.	27.0
Protothaca staminea (Conrad, 1837)	16.3
Tresus capax (Gould, 1850)	6.6
Gari californica (Conrad, 1837)	4.3
Saxidomus giganteus Deshayes, 1839	3.9
Haliotis kamtschatkana Jonas, 1845	2.8
Chlamys hastata (Sowerby, 1842)	1.5
Macoma sp.	1.4
Polinices lewisii (Gould, 1847)	1.1
Hinnites giganteus (Gray, 1825)	1.0
Semele rubropicta Dall, 1871	0.9
Pugettia sp.	0.8
Diplodonta orbellus (Gould, 1852)	0.8
Humilaria kennerlyi (Reeve, 1863)	0.7
Panopea generosa (Gould, 1850)	0.6
Telmessus cheiragones[1] (Tilesius, 1815)	0.4
Modiolus rectus (Conrad, 1837)	0.3
Pododesmus cepio (Gray, 1850)	0.2
Diodora aspera (Rathke, 1833)	0.2
Solen sicarius (Gould, 1850)	0.1
Crepidula sp.	0.1
Strongylocentrotus[2] sp.	0.03
Lyonsia saxicola	0.03
Other Items[3]	0.14

[1]Crustacea
[2]Echinodermata
[3]These included traces of limpets (Acmaeidae), unidentified crabs, and occasionally octopuses.

same area were feeding on different prey as indicated by shell collections from dens. For example, one octopus began to feed heavily on the bivalve *Diplodonta orbellus* (60% of the prey items at its den) but the same diet was not observed in other dens nearby. In one study site in Clayoquot Sound, octopuses fed mainly on *Clinocardium nuttallii, Cancer productus* and *Protothaca staminea* while 2 octopuses in that area were feeding heavily on the bivalve *Gari californica* (46% and 32% of 100 and 62 items, respectively). In these 2 cases the clam *G. californica* occurred frequently in the diet throughout the whole summer. The octopus making heaviest use of such clams also fed more on the clam *Saxidomus giganteus* (9%) than octopuses in nearby dens. In another study site in Clayoquot Sound, octopuses made considerable use of the commercially important Dungeness crab *Cancer magister*. For

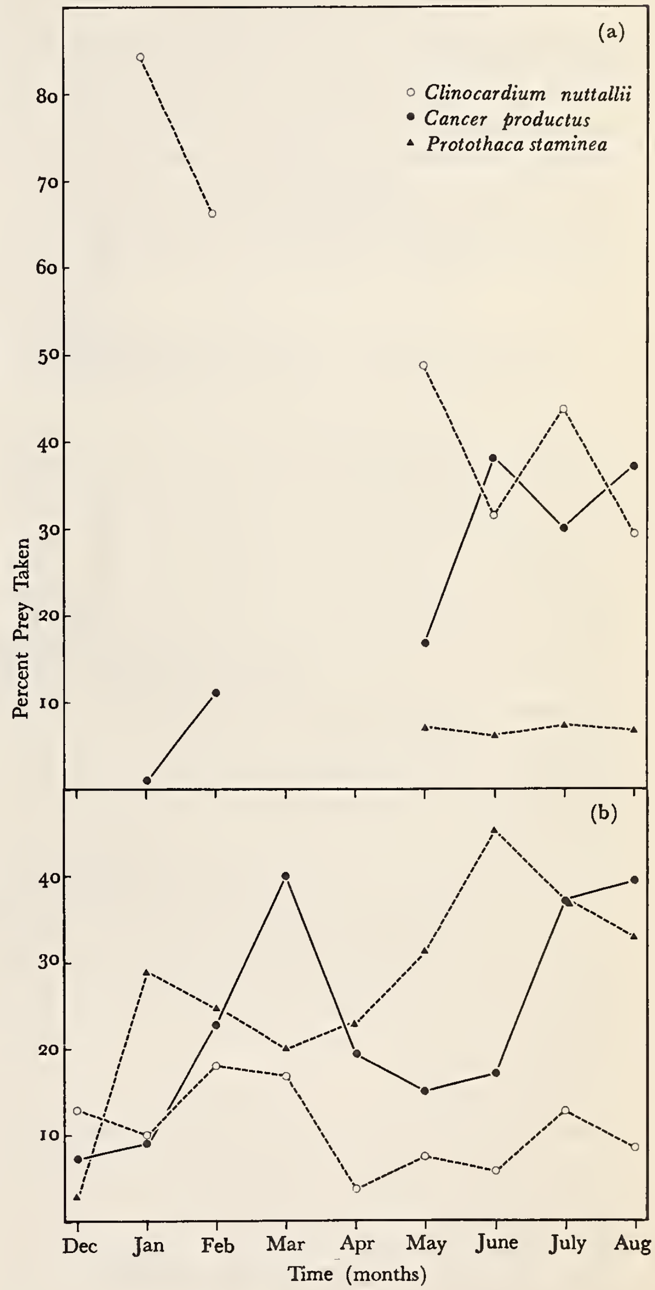

Figure 1

Variation in the percentage of selected prey in the diet of octopuses in Clayoquot (a) and Barkley Sounds (b) based on shells collected from den entrances example, in 1 den, 27 of 100 prey items consisted of these crabs. Another den nearby however, showed heavy use (42%) of the rock crab (*C. productus*) over the same period.

The idea of individual differences in octopus feeding was also supported by a multiple regression analysis relating the percent crabs in the diet to den site, depth and time of year. Den site, presumed to represent an individual octopus, and time of year were significant factors ($p<0.01$). However, the regression explained at most only 28% of the variation in crab use. Unfortunately no quantitative estimates of crab availability were made for the study sites so that this important variable was not included in the analysis.

FORAGING AREA AND FOOD SELECTION

Although octopuses were only rarely observed feeding, the items in the diet and the characteristics of the habitat provide some information on their foraging. The composition of the diet indicates that foraging occurs more often on soft bottoms than on rock surfaces. The absence of mussels (*Mytilus* spp.) in the diet, in spite of their abundance in the intertidal zone, may indicate an avoidance of either mussels themselves or the rocky intertidal habitat in which they are found. Most of the octopus dens in Clayoquot Sound were close to eel grass beds where cockles *Clinocardium nuttallii* were available in great abundance. Frequent foraging trips to such eel grass beds would explain the high percentage of these items in the diet. Octopuses making heavy use of *Protothaca staminea* had dens located near gravel beaches where these clams are found. Both *C. nuttallii* and *P. staminea* are found close to the surface of the sediments and are presumably easy to obtain by octopuses. Bivalves found deep in the sediment were utilized less. Thus, octopuses fed very little on geoducks (*Panopea generosa*) in spite of their great abundance in the area and their occurrence in a variety of types of bottoms.

There is evidence that octopuses do not feed upon some potential prey close to their dens. *Haliotis kamtschatkana* was not heavily preyed upon and in many cases this species was observed close to octopus dens, even at the entrance. Similarly, the rock scallop *Hinnites giganteus* was often present near dens but was ignored at least temporarily. In one den, seven of these were attached near the den opening.

Certainly, based on qualitative impressions, the low use of prey like *Hinnites giganteus*, *Haliotis kamtschatkana* and *Panopea generosa* did not reflect a low abundance of these prey. In fact, since the time of the study, commercial harvesting of *P. generosa* has been initiated in the area because of its great abundance.

SIZE OF PREY

Collections of shells from dens indicated that prey size varied over a wide range. Sizes of the bivalve *Protothaca staminea* taken by octopuses varied from 15.5 mm. to 70 mm. The size distribution of eaten clams was unimodal with a peak in the 40-45 mm size class (Figure 2). The size distributions of these clams were similar in shell collections from both Barkley and Clayoquot Sounds. Sizes of abalone (*Haliotis kamtschatkana*), butter clams (*Saxidomus giganteus*) and crabs (*Cancer* spp.), all of commercial importance, taken as prey also varied over a wide range. For all 3 types of prey, the sizes taken most frequently were in the range 75-95 mm (Figure 2). The only information on sizes of these prey available in the habitat is from an abalone survey reported by QUAYLE (1971) in one of the octopus study sites. The survey was carried out in 1963 and indicated a mean length of 108 mm with a range of 66-137 mm. However, abalone have been commercially harvested along with red sea urchins *Strongylocentrotus franciscanus* (A. Agassiz, 1863) in the area since that time. No information is available on current size distribution.

Figure 3 shows that the mean size of all prey together increased with increasing size of octopus ($p < 0.05$). Similarly, size of *Clinocardium nuttallii* increased with size of octopus ($p < 0.05$) although the relationship was not significant for *Protothaca staminea*. In spite of the statistical significance, considerable variability was present in sizes taken by octopuses of different sizes. However, further support comes from current feeding experiments with a very small octopus which selects small prey from a variety of sizes available (S. Robinson, personal communication).

GROWTH RATES IN THE FIELD

Recaptures of tagged octopuses provided growth data under natural conditions. The weight changes for 15 tagged octopuses are given in Table 2. The gain in weight per day varied from 13.9 g to 109.4 g. When expressed as a fraction of the mean weight during the observation period, these gains indicated daily growth rates varying from 0.1 to 1.8 percent.

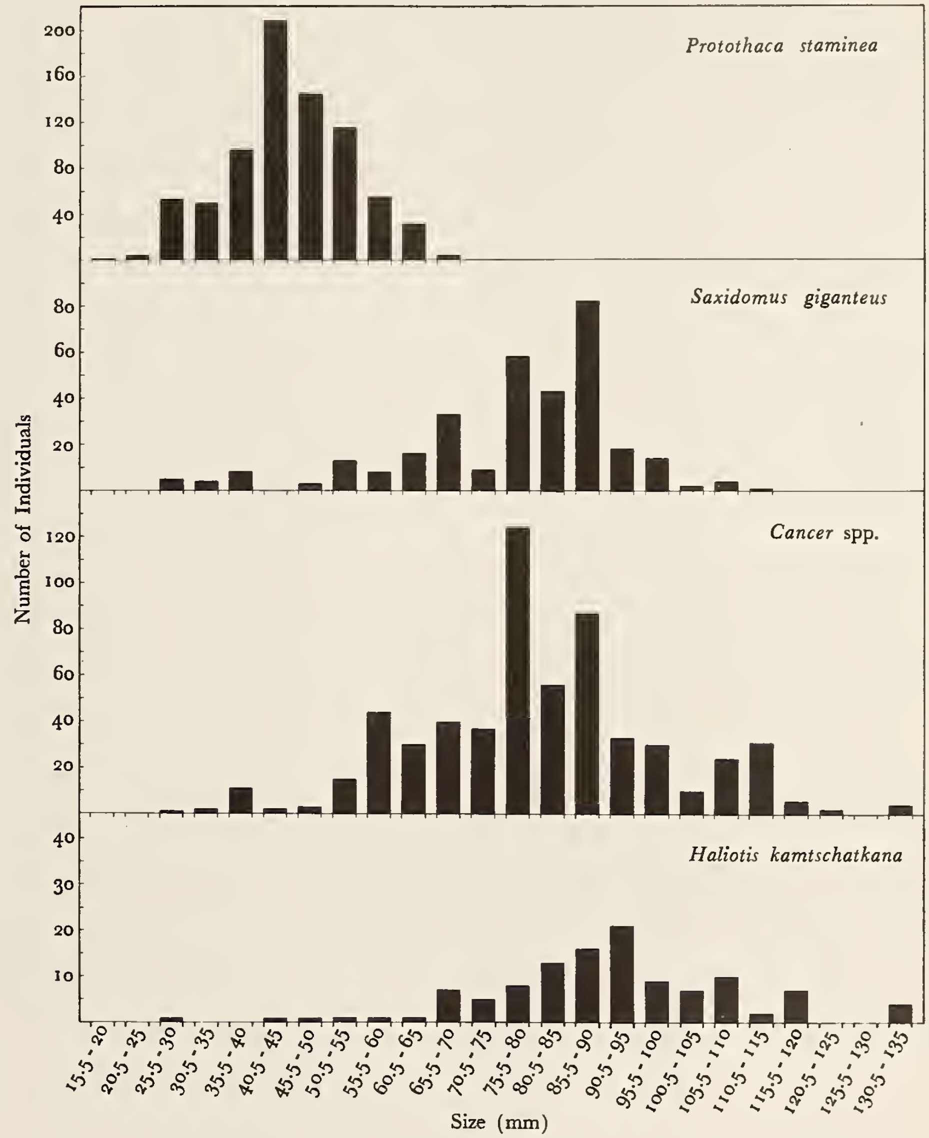

Figure 2

Size frequency histograms for commercially important prey species taken by octopuses

Average daily growth rates appeared to be relatively high in October (0.8-0.9), lower over the winter (0.1-0.6) and high again in spring and summer (0.5-1.8). This seasonal pattern is also evident when weights of individuals recaptured several times are examined (Table 3).

GROWTH RATES AND FEEDING OF CAPTIVE OCTOPUSES

The 2 octopuses in the large tanks in summer 1977 showed similar exploratory behaviour and prey manipulation

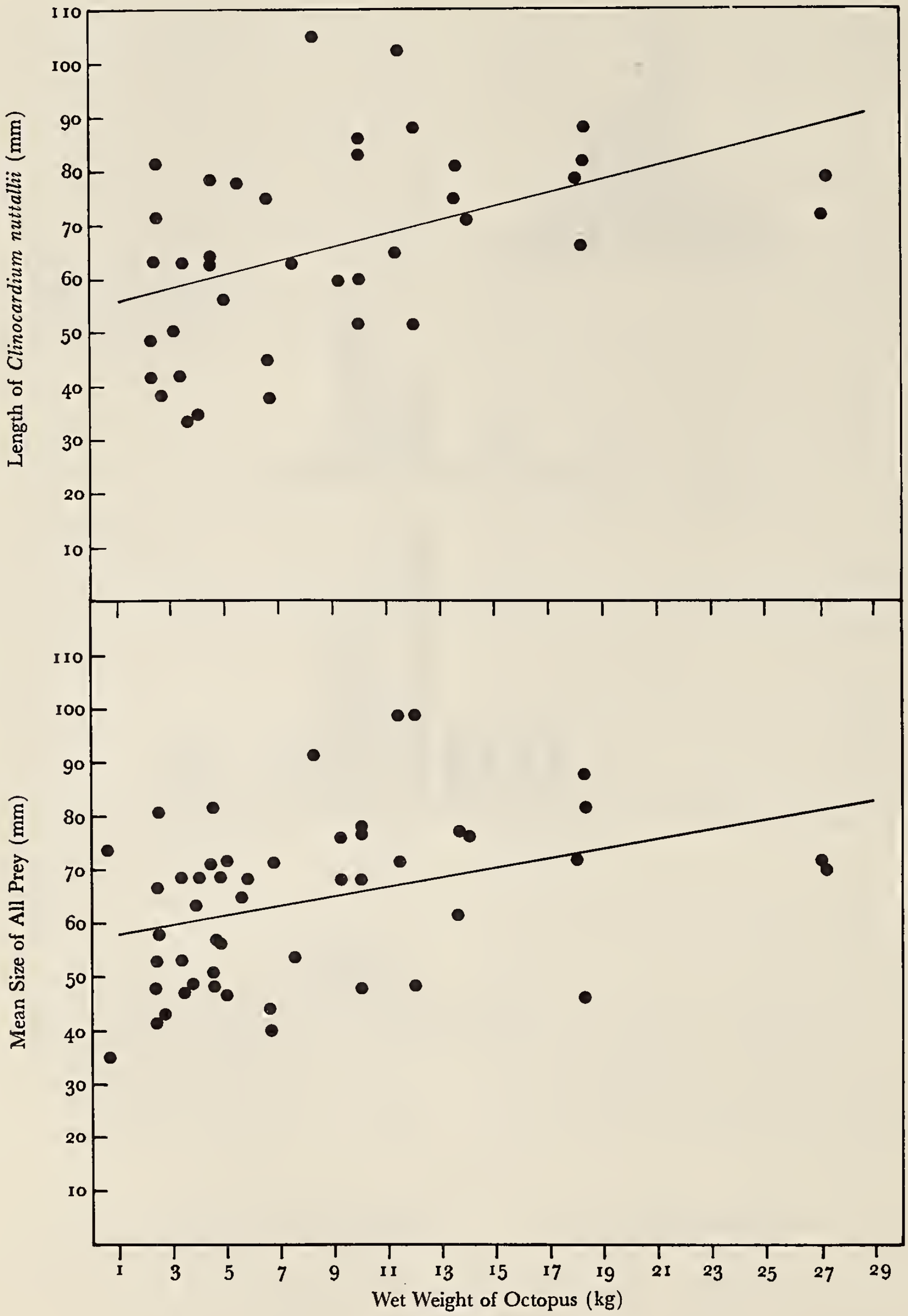

Figure 3

The relationship between size of octopus and size of prey based on wet weights of octopuses and length or maximum diameter of prey. The line was fitted by standard regression techniques

Table 2

Growth rates of tagged octopuses recaptured in Clayoquot Sound. Octopuses 1-4 and 12 were tagged in 1978, all others in 1979.

Octopus	Sex	Observation period in days	Initial weight (kg)	Final weight (kg)	Gain in weight/day (g)	Average daily growth rate (%)
1	F	16 (Oct.)	9.5	10.8	78.1	0.8
2	F	16 (Oct.)	12.0	13.8	109.4	0.9
3	F	118 (Oct.-Feb.)	10.5	18.4	66.9	0.5
4	M	82 (Oct.-Jan.)	10.3	17.4	86.6	0.6
5	M	36 (Jan.-Feb.)	15.7	16.7	27.8	0.2
6	F	36 (Jan.-Feb.)	16.4	17.4	27.8	0.2
7	F	36 (Jan.-Feb.)	17.9	20.2	63.9	0.3
8	F	109 (Jan.-April)	11.4	16.3	44.9	0.3
9	F	36 (Jan.-Feb.)	10.7	11.2	13.9	0.1
10	F	73 (Feb.-April)	11.2	13.7	33.6	0.3
11	F	67 (April-June)	8.9	13.6	70.2	0.6
12	F	210 (Oct.-May)	6.3	13.3	33.3	0.3
13	F	12 (July)	7.5	8.8	108.3	1.3
14	M	14 (July-Aug.)	2.9	3.8	60.7	1.8
15	F	25 (July-Aug.)	13.4	15.3	74.0	0.5

Table 3

Growth of tagged octopuses recaptured at different times of the year.

Octopus (from table 2)	Sex	Observation period in days	Initial weight (kg)	Final weight (kg)	Gain in weight/day (g)	Average daily growth rate (%)
3	F	16 (Oct.)	10.5	12.9	150.0	1.3
		66 (Oct.-Jan.)	12.9	17.2	65.2	0.4
		36 (Jan.-Feb.)	17.2	18.4	33.3	0.2
8	F	36 (Jan.-Feb.)	11.4	12.2	22.2	0.2
		73 (Feb.-April)	12.2	16.3	56.2	0.4
11	F	35 (April-May)	8.9	11.3	67.1	0.7
		32 (May-June)	11.3	13.6	73.4	0.6

when freshly caught bivalves were placed in the aquaria. Shells were momentarily grasped and then either dropped or held; all were usually touched even if they were not eaten. Often several bivalves were gathered under the webbing at the same time and carried to either an artificial den or a 'preferred' corner. At times the bivalves were eaten where they were found. Approximately 30% of the shell debris was scattered in other parts of the tanks, the rest being at the den.

The following bivalves were presented to captive octopuses in various combinations: *Tresus capax, Siliqua patula* (Dixon, 1789), *Humilaria kennerlyi, Mytilus cali-*

fornianus Conrad, 1837, *Mya arenaria* Linnaeus, 1758, *Protothaca staminea,* and *Saxidomus giganteus.* All of these bivalve species were fed on at least once by the captive octopuses even though *Mytilus californianus* and *Mya arenaria* did not show up in shell collections from natural dens. When all were presented at once to an octopus, the soft shelled clam (*M. arenaria*) and the gaper clam (*Tresus capax*) were eaten before both *P. staminea* and *S. giganteus.* This occurred even though all were first examined by the octopus, and in spite of the fact that the latter two are most frequent in the diet of wild octopuses. This apparent preference occurred in 5 separate experiments. In one case, a captive octopus attacked and consumed both a *M. arenaria* (length 8.8 cm) and a *T. capax* (length 11.3 cm) in 2 hours. The shell of *M. arenaria* was cracked open, while that of the *T. capax* appeared to simply have been pried apart with no effect on the shell. Drill holes were commonly observed in shells of *P. staminea* fed on by the captive octopuses.

In the studies carried out in the fall of 1978, octopuses held in boxes suspended in the inlet were fed *ad libitum* with fish (*Merluccias productus*), crabs (*Pugettia producta),* abalone (*Haliotis kamtschatkana)* and bivalves (*Protothaca staminea* and *Mya arenaria*). In almost all cases the fish was eaten first, then crabs, followed by the soft shelled clam *M. arenaria* and finally the other prey items. Prey handling was observed through the plexiglas bottom of the holding box. When handling the crabs (*P. producta*) the octopus first attempted to pull the carapace off. If this failed, the octopus would turn the crab ventral side up and drill the abdomen of the crab (9 out of 15 cases). Female crabs were drilled more often than males (77%, n = 18; 33%, n = 12). Handling of *M. arenaria* was similar to that observed in the experiments in summer 1977. *M. arenaria* was pulled apart or cracked open while *P. staminea* was drilled.

All captive octopuses grew over the fall 1978 observation period, including those in the box in the inlet as well as those in the aquaria. Average daily growth rates varied from 0.6% to 1.1% (Table 4). The average conversion ratio was 1.7:1.

Since growth was frequently measured it was possible to detect variation in food intake with changing composition of available prey. In all cases octopuses ate more food relative to their body weight when fish and crabs were available than when only crabs were available. For example, octopus number 3 (Table 4) consumed 1.3% of its body weight per day when fish and crabs were available, and only 0.95% when crabs alone were present.

DISCUSSION

Models of optimal foraging for refuging predators have indicated that such predators will adopt search patterns that locate feeding patches some distance away from the refuge rather than ones nearby (Morrison, 1978). According to Morrison, such tactics might explain why natural predators seem to ignore nearby prey, and why foraging ranges of some animals can be so broadly overlapping. *Octopus dofleini* is a refuging predator leaving its den usually at night (personal observations) to go on foraging trips, and often ignoring potential prey items near the den itself. The appearance of considerable numbers of *Protothaca staminea* in the diet suggests that *O. dofleini* may make continuing use of particular feeding sites since

Table 4

Growth and food intake of 6 captive octopuses.
The first 4 octopuses were kept in the laboratory while 5 and 6 were in boxes submerged in an inlet.

Octopus	Observation period (days)	Initial weight (kg)	Gain in weight/day (g)	Average daily growth rate (%)	Daily feeding rate (%)	Daily feeding rate (g/day)	Food conversion (%)	Food conversion (ratio)
1	60	2.8	22.5	0.7	1.2	(39.5)	39.6	(2.5:1)
2	60	2.8	41.7	1.0	1.2	(53.6)	74.7	(1.3:1)
3	40	2.5	33.8	1.1	1.4	(45.9)	73.6	(1.4:1)
4	40	2.8	37.5	1.1	1.2	(43.2)	87.0	(1.2:1)
5	45	4.0	44.4	0.9	2.0	(100.4)	44.3	(2.3:1)
6	42	3.3	21.4	0.6	1.3	(48.6)	44.1	(2.3:1)

this clam occurs in discrete intertidal gravel beds some distance from the dens. Thus, *O. dofleini* acts like many predators faced with patchy prey distributions and a refuging mode of life (Morrison, 1978).

The observation that several clams were picked up at one time by captive octopuses makes energetic sense and agrees with the observations of Yarnall (1969) who reported that *Octopus cyaneus* transported several crabs at one time. The wide variety of prey items in the diet of *O. dofleini* suggests that it is an opportunistic feeder. Nevertheless, the items occurring most frequently in the diet are those that are numerous and readily accessible like *Clinocardium nuttallii* and *Protothaca staminea* which occur in dense populations close to the surface of the sediments. Considerable feeding on *P. staminea* has also been reported for *O. bimaculatus* by Fotheringham (1974), who suggested that octopuses might act as keystone predators in the same manner as *Pisaster ochraceus* (Brandt, 1835) in *Mytilus* beds (Paine, 1966). However, at the present time there are no data to support his contention. As in the present study, Fotheringham also found little or no use of the mussel *Mytilus* spp. by octopuses in spite of the abundance of this potential prey item. Nevertheless, captive *O. dofleini* will feed readily on these and other items uncommon in their natural diet, especially if they are easy to break open and feed upon. Hartwick *et al.* (1968c) showed that prey handling by *O. dofleini* involved breaking apart shells, pulling them apart, or drilling and, in this regard, these octopuses were similar to other species (Pilson & Taylor, 1961; Arnold & Arnold, 1969, Wodinsky, 1969). The apparent preferential selection of particular food items, like *Mya arenaria* which does not require drilling, over other bivalves and the individual variation in diet shown in the field presumably reflect the learning capabilities of these organisms (Wells, 1978).

Although fish remains were usually not found at den sites, they may be taken as prey. Their absence from den collections may indicate that scavengers quickly remove any remains or that they are fed on away from the den. Observations in the laboratory indicated that most prey were taken to the den, although up to 30% may be scattered some distance away. During the present study one octopus was observed feeding on a crab in the open away from any den sites, and occasionally small areas have been found with an accumulation of shells possibly indicating feeding by an octopus. Thus, shell collections at dens may provide an incomplete picture of the diet of octopuses. Long foraging trips by octopuses and the existence of resting and feeding sites away from dens have been noted in other studies (Yarnall, 1969; Hoghberg & Cough, 1971).

Although the relationship between prey size and size of octopus is admittedly weak, current studies with small individuals provide support for the idea. The relationship may only apply to prey items like cockles, *Clinocardium nuttallii*, which are typically broken apart rather than drilled. Larger cockles are presumably more difficult to handle and are fed on more frequently by larger octopuses. However, it may be that over the range of sizes considered in the present study, there is no real size effect and certainly, further work on the matter is called for.

Both food intake and growth of octopuses are affected by temperature (Mangold & Boletzky, 1973). In the cold waters off Vancouver Island (7.5° C - 15° C surface temperature), *Octopus dofleini* showed growth rates comparable to those reported for *O. vulgaris* kept in constant temperatures of 10° C (Mangold & Boletzky, 1973). Daily growth rate of *O. vulgaris* at 10° C varied from 0.35 to 1.57% while that of tagged *O. dofleini* in the present study ranged from 0.1 to 1.8%.

Growth rates in both field and laboratory conditions in the present study were comparable, although only one octopus in the tagged population was as small as those in the laboratory and its growth rate was in fact higher (1.8% compared to 1.1% or less). The possible sources of differences in growth in laboratory octopuses compared with free living octopuses have been discussed by Joll (1977).

A careful examination of Table 2 indicates that growth rates and food intakes are lower for larger octopuses when comparisons are made at the same time of year. This agrees with data presented for *Octopus cyaneus* by Van Heukelem (1973). The data on tagged *O. dofleini* indicate that an octopus weighing between 6 and 11 kg. may double its weight in just over a 5 month period. Since sizes of octopuses in the field study were not comparable to those in the laboratory, it is not clear whether the field rates were maximal or whether food was limiting. The high average daily growth rate of one small octopus in the field suggests that at least in that study area food is plentiful. Although Joll (1977) suggests that it is unlikely that octopuses in the field live in a condition of excess food supply, Wells (1978) refers to data from experiments which indicate that food availability is probably not a limiting factor. The present results appear to confirm this.

Joll (1977) suggests that daily feeding rates of *Octopus tetricus* need to be 2% or more to satisfy their maintenance requirements, and that gross growth efficiencies under those conditions range from 11 to 76% (9.1:1 to 1.3:1) with a mean of 46.8% (2.1:1). Van Heukelem (1976) estimates the gross growth efficiency for *O. cyaneus* and *O. maya* to be 38.3% and 39.5%, respectively, but suggests that on a caloric basis these figures may be as high as 60%.

In the present study gross growth efficiencies ranged from 39.6 to 87% (2.5:1 to 1.2:1) with daily growth rates from 0.6 to 1.1%. The range in gross growth efficiency is similar to that reported for *O. vulgaris* by MANGOLD & BOLETZKY (1973).

Although growth data are lacking for the planktonic juveniles, nevertheless, the present study does permit some speculation on the possible lifespan of *Octopus dofleini*. The growth information recorded during the present study covers the range from 2.5 to 20.2 kg. By placing weight changes in consecutive order an estimate of time for growth over the total range is obtained. This comes to 470 days. Depending on the growth rate at early stages *O. dofleini* may take between 2 and 3 years to reach maximum size. This estimate may be modified after current tagging and growth studies are completed.

ACKNOWLEDGMENTS

We wish to thank William Blaylock and David Parker for their help during the study. Thanks also to Gary Thorarrinson and Matt Blackman for help in diving and to two anonymous referees for their useful comments. Special thanks to the McLories of Tofino for their hospitality. This work was supported by Fisheries and Oceans, Environment Canada and by the Natural Sciences and Engineering Research Council Canada.

Literature Cited

ALTMAN, J. S.
1967. The behavior of *Octopus vulgaris* Lamarck in its natural habitat: a pilot study. Underwater Assoc. Rprt. 1966-1967: 77-83
ARNOLD, JOHN MILLER & KRISTIN OKERLUND ARNOLD
1969. Some aspects of hole-boring predation by *Octopus vulgaris*. Amer. Zool. 9: 991-996
FOTHERINGHAM, NICK
1974. Trophic complexity in a littoral boulder-field. Limnol. Oceanogr. 19: 84-91
HANLON, R. T.
1977. Laboratory rearing of the Atlantic reef octopus, *Octopus briareus* Robson, and its potential for mariculture. World Maricult. Soc. 8: 471-482
HARTWICK, E. B., P. A. BREEN & L. TULLOCH
1978a. A removal experiment with *Octopus dofleini* (Wülker). Journ. Fish. Res. Brd. Canada 35 (11): 1492-1495
HARTWICK, E. B., G. THORARINSSON & L. TULLOCH
1978b. Antipredator behaviour in *Octopus dofleini* (Wülker). The Veliger 21 (2): 263-264 (1 October 1978)
1978c. Methods of attack by *Octopus dofleini* (Wülker) on captured bivalve and gastropod prey. Mar. Behav. Physiol. 5: 193-200
HIGH, W. L.
1976a. The giant Pacific octopus. Mar. Fish. Rev. 38 (9): 17-22
1976b. Escape of Dungeness crabs from pots. Mar. Fish. Rev. 38 (4): 19-23
HOCHBERG, F. G. & J. A. COUCH
1971. Biology of cephalopods. Tektite II, Scientists in the Sea, U. S. Dept. Inter., Mission 8-50: pp. VI, 221-228
JOHNSON, MARTIN W.
1942. Some observations on the feeding habits of the octopus. Science 95 (2471): 428-479
JOLL, L. M.
1977. Growth and food intake of *Octopus tetricus* (Mollusca: Cephalopoda) in aquaria. Austral. Journ. Mar. Freshwater Res. 28: 45-56
KAYES, R. J.
1974. The daily activity pattern of *Octopus vulgaris* in a natural habitat. Mar. Behav. Physiol. 2: 337-343
KYTE, MICHAEL A. & GREGORY W. COURTNEY
1977. A field observation of aggressive behavior between two North Pacific Octopus, *Octopus dofleini martini*. The Veliger 19 (4): 427-428; 1 plt. (1 April 1977)
MANGOLD, KATHARINA & SIGURD VON BOLETZKY
1973. New data on reproductive biology and growth of *Octopus vulgaris*. Mar. Biol. 19: 7-12
MATHER, JENNIFER A.
1980. Some aspects of food intake in *Octopus joubini* Robson. The Veliger 22 (3): 286-290; 3 text figs. (1 January 1980)
MORRISON, DOUGLAS W.
1978. On the optimal searching strategy for refuging predators. Amer. Natural. 112: 925-934
MOTTET, MADELON GREEN
1975. The fishery biology of *Octopus dofleini* (Wülker). Wash. Dept. Fish. Tech. Rprt. 16: 1-39
NIXON, MARION
1966. Changes in body weight and intake of food by *Octopus vulgaris*. Journ. Zool. London 150: 1-9
1969. The lifespan of *Octopus vulgaris* Lamarck. Proc. Malac. Soc. London 38: 529-540
1979. Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. Malacologia 18: 431-443
PAINE, ROBERT TREAT
1966. Food web complexity and species diversity. Amer. Natur. 100: 65-75
PENNINGTON, H.
1979. Octopus fishing techniques and gear. Alaska seas and coast 7 (3): 1-5
PILSON, M. E. Q. & P. B. TAYLOR
1961. Hole drilling by *Octopus*. Science 134 (3487): 1366-1368
QUAYLE, DANIEL BRANCH
1971. Growth, morphometry and breeding in the British Columbia abalone (*Haliotis kamtschatkana* Jonas). Fish. Res. Brd. Canada, Tech. Rprt. No. 279: 84 pp.
VAN HEUKELEM, WILLIAM F.
1973. Growth and lifespan of *Octopus cyanea* (Mollusca: Cephalopoda). Journ. Zool. London 169: 299-315
1976. Growth, bioenergetics and lifespan of *Octopus cyanea* and *Octopus maya*. Ph. D. Thesis, Univ. Hawaii
WELLS, MARY JANE
1978. Octopus. Physiology and behaviour of an advanced invertebrate. Chapman & Hall, London, 417 pp.
WODINSKY, JEROME
1969. Penetration of the shell and feeding on gastropods by *Octopus*. Amer. Zoologist 9: 997-1010
WOODS, J.
1965. Octopus watching off Capri. Animals 7 (12): 324-327
YARNALL, J.
1969. Aspects of the behaviour of *Octopus cyanea* Gray. Anim. Beh. 17: 755-759